Use of different statistical models to predict direct genomic values for productive and functional traits in Italian Holsteins

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Summary

One of the main issues in genomic selection is the huge unbalance between number of markers and phenotypes available. In this work, principal component analysis is used to reduce the number of predictors for calculating direct genomic breeding values (DGV) for production and functional traits. 2,093 Italian Holstein bulls were genotyped with the 54K Illumina beadchip and 39,555 SNP markers were retained after data editing. Principal Components (PC) were extracted from SNP matrix and 15,207 PC explaining 99% of the original variance were retained and used as predictors. Bulls born before 2001 were included in the reference population, younger animals in the test population. A BLUP model was used to estimate the effect of principal component on Deregressed Proof (DRPF) for 35 traits and results were compared to those obtained by using SNP genotypes as predictors either with BLUP or Bayes_A models. Correlations between DGV and DRPF did not substantially differ among the three methods except for milk fat content. The lowest prediction bias was obtained for the method based on the use of principal component. Regression coefficients of DRPF on DGV highlighted a relevant difference between methods being lower than one for the approach based on the use of PC and higher than one for the other two methods. The use of PC as predictors resulted in a high reduction of number of predictors (about 38%) and of computational time that was about the 9% of the time needed to estimate SNP effects with the other two methods. Accuracies of genomic predictions were in most of cases slightly higher than those of the traditional pedigree index.

Introduction

Genomic Selection (GS) allows for an early prediction of the genetic merit of selection candidates by combining genotypes of biallelic SNP markers and phenotypes (Meuwissen *et al.* 2001). In GS programs, the effects of a large number of SNP on the considered trait is estimated from a reference (REF) population and then used to predict Direct Genomic Values (DGV) in a test (TEST) population where only marker information is available (Meuwissen *et al.* 2001).

The switch from traditional to GS breeding programmes should be justified by a higher reliability of DGV predictions compared to parent average (PA). Actually, DGV accuracy is primarily influenced by the REF population size and, to a lesser extent, by the estimation method. Early simulation studies highlighted that a few thousands of animals are needed in order to obtain DGV accuracies of 0.7 (Hayes *et al.* 2009b) and that about 30,000 unrelated individuals should be considered as REF to estimate DGV with the 800K chip (Meuwissen 2009). Such figures are rather difficult to achieve in practice, even in the case of major cosmopolite breeds and large international GS projects. Even in the USA, where the Holstein population is larger than in other countries, the REF population size in December 2010 was 16,293 (Wiggans 2011). Actually most studies on Holstein cattle have dealt with REF populations of about one (Berry 2009) or few thousands of animals (VanRaden *et al.* 2009; Habier *et al.* 2010; Liu 2011; Schenkel 2009; Su *et al.* 2010).

The increase of REF population size just by new genotyping is still rather expensive. This situation will be further exacerbated by the use of denser SNP platforms (i.e. 800K) or the whole genome sequence. Cooperation across countries represents a effective way to enlarge the size of reference population. Some experience has already been done. For example, United States, Canada, Italy and Great Britain shared their data (Olson 2011; VanRaden *et al.* 2011) and in Europe the EuroGenomics project allowed Germany, France, The Netherlands and Denmark, Finalnd and Sweden to join their datasets and obtain a REF population of about 18,000 bulls {Lund, 2011

#7516} . Similar experiences have occurred also in other breeds, as the Brown Swiss with the Intergenomics project (B. Zumbach *et al.* 2010).

Apart from the mathematical algorithms, the difference between methods used to predict DGV is mainly in the assumption on marker effect distribution. The BLUP approach fits an equal contribution of each SNP to the genetic variance of the trait (Meuwissen *et al.* 2001). It is equivalent to the use of an animal model with the additive genetic effect structured by the genomic relationship matrix {Hayes, 2009 #389}. On the other hand, Bayesian methods allow genetic variance to differ across chromosome segments, assuming that few SNPs have a large effect and many SNPs have a small effect on the trait, respectively (Hayes *et al.* 2009a; Meuwissen *et al.* 2001; Su *et al.* 2010). Both approaches may implement a mixed inheritance by including a polygenic effect structured by pedigree relationship matrix to explain a part of the genetic variance (Habier *et al.* 2010; Berry 2009). In early studies based on simulated data, Bayesian methods usually outperformed BLUP (Meuwissen *et al.* 2001; Clark *et al.* 2011). On real data, such differences are no longer detectable except for traits for few genes with a larger effect has been detected (Hayes *et al.* 2009a; VanRaden *et al.* 2009).

A further issue on GS is represented by the adoption of techniques for reducing the huge unbalance between the number of phenotypes and genotypes available. It represents a basic requirement in the implementation of GS program in populations of limited size. However, reduction of predictor dimensionality may also be useful for large populations, as the Holstein breed, with the perspective of using a 800K SNP chip or the complete sequence in the near future. SNP pre-selection based on the relevance to the trait or the use of dimension reduction multivariate methods as principal component analysis (PCA) (Solberg *et al.* 2009; Macciotta *et al.* 2010; Vazquez *et al.* 2011, Pintus *et al*., 2012) and partial lest squares regression (Moser *et al.* 2009; Vazquez *et al.* 2011) represent the two main strategies adopted to address this issue). Compared to

SNP pre-selection, PCA reduction does not discard any SNP and the reduced panel of predictors is independent from the trait considered.

In this work, DGV of different production and functional traits for a sample of Italian Holstein bulls obtained by joining data generated in two GS research projects were predicted by using different types of predictors, i.e. the SNP genotypes or the scores of a reduced number of principal components. Moreover, also the assumptions on predictor effect are compared by using a Bayesian or a BLUP method.

Materials and methods

Data

Genotypes of 2,093 Italian Holstein bulls were generated in two Italian research projects: the SELMOL and the PROZOO. Birth years of the bulls ranged from 1979 to 2007, with an average number of 72 animals per year. Bulls born before or after 2001 were included in the REF and TEST populations, respectively. Distribution of REF and TEST bulls across birth years is illustrated in Figure 1

Animals were genotyped using the BovineSNP50 BeadChip (Illumina, San Diego, CA). Data editing procedure has been performed. SNP were discarded based on missing data (>0.025), minor allele frequency <0.05), existence of Mendelian inheritance conflicts, absence of heterozygous genotypic class, deviance from Hardy-Weimberg equilibrium (<0.01 bonferroni corrected). (Wiggans *et al.* 2009). Markers retained after edits were 39,555. Missing SNP alleles were replaced by the most frequent allele at that specific locus. A total of 86 bulls were discarded: 48 samples were replicates or had inconsistent mendelian inheritance information, whereas 38 samples had low overall call rate (>1000 missing SNPs).

Phenotypes were Deregressed EBV (DRPF) provided by the Italian Holstein Association ANAFI. Thirty-five productive and functional traits have been considered (Table 1). Not all phenotypes were available for all bulls, thus small differences in sizes of REF and TEST populations across traits occurred. On average, sizes of REF and TEST populations were of 1,314 and 624 bulls, respectively, . For each traits, heritability, number of REF and TEST bulls and average reliability of DRPF are reported in table xx

Methods

Methodologies used to calculate DGV differed in the dimensionality of predictors (SNP genotypes vs. PC scores) and in the assumptions on marker effect distributions (BLUP vs Bayes_A).

Reduction of predictor dimensionality by Principal Component Analysis

PCA were used to extract latent variables from the SNP matrix (n x m) (where n=total number of animals, and m=number of SNPs retained after edits). Genotypes were coded as $-1/\sqrt{2p_i(1-p_i)}$ and $1/\sqrt{2p_i(1-p_i)}$ for two different homozygotes and 0 for heterozygotes, respectively, where p_i is the frequency of one of the two allele at locus *i*.{Luan, 2009 #230}. Principal components were extracted separately for each chromosome for computational reasons. Previous studies based on simulated data reported the same DGV accuracy for PCA carried out on the entire genome or separately per chromosome (Macciotta *et al.* 2010). The number of components to retain was based on the amount of original variance explained, calculated as sum of eigenvalues. In particular, five thresholds with regard to the amount of variance explained were considered with a corresponding number of extracted variables ranging from about 2,600 to 15,200

(Figure 2). Component scores for each animal were used as predictors in the further steps of DGV calculation and validation.

BLUP

The effect of predictors, either SNP (SNP_BLUP) or principal component scores (PC_BLUP), on phenotypes of the REF bulls was estimated with the following mixed linear model

$$\mathbf{y} = \mathbf{1}\,\mu + \mathbf{Zg} + \mathbf{e} \qquad [1]$$

where **y** is the vector of Deregressed EBV, **1** is a vector of ones, μ is the general mean respectively, **Z** is the matrix of SNP genotypes or PC scores, **g** is the vector of their effects treated as random, and **e** is the vector of random residuals. Covariance matrices of random effects (**G**) and residuals (**R**) were modelled as diagonal $\mathbf{I}\,\sigma_{gi}$ and $\mathbf{I}\,\sigma_e^2$ respectively, where λ is σ_e^2/σ_{gi}^2 (where $\sigma_{gi}^2 = \sigma_a^2/n$ PC) assuming an equal contribution of each predictor to the additive genetic variance. Additive genetic σ_a^2 and residual σ_e^2 variances for all traits were provided by the Holstein association. BLUP solutions were estimated using Henderson's normal equations (Henderson 1985) and mixed model equations were solved using a Gauss-Seidel residual update (GSRU) iterative algorithm (Legarra and Mistzal, 2008)

BAYES_A

A Bayes A method (BAYES_A) that assumes that most of markers have very small effects (e.g. markers not linked to any QTL) and only few have large effects was fitted to the REF data set with the same structure used in model [1]. Prior distributions and parameters where chosen according to Meuwissen *et al.* (2001). Twenty thousand iterations were performed, the first 10,000

were taken as burn in and thus discarded, and all the others were kept. A residual updating algorithm was used to solve the model (Legarra *et al.* 2008).

DGV estimation

DGVs in the TEST population were calculated using the general mean ($\hat{\mu}$) and the vector ($\hat{\mathbf{g}}$) of the solution of predictors effects estimated with BLUP or BAYES_A in the previous step as:

$$\mathrm{DGV_k} = \hat{\mu} + \sum_{i=1}^{m} \mathbf{z}'_{ik}\, \hat{\mathbf{g}}_i$$

where **z** is the vector of PC scores or marker genotypes and *m* is the number of PC or markers used in the analysis.

The accuracy of direct genomic values DGV was assessed in TEST individuals by calculating Pearson correlations between DRPF and DGV. Bias were assessed by examining regression of DRPF on predicted DGV. Goodness of prediction was evaluated also by calculating the mean squared error of prediction (MSEP) and by its partition in different sources of variation related to systematic and random errors (Tedeschi 2006). Moreover, the accuracy of genomic predictions was compared to the realized accuracies of 2005 pedigree indexes (PI) of TEST individuals for some traits. PI from 2005 were chosen because nearly all animals in the TEST population did not have daughter records at that time.

Results

The effect of different thresholds of explained variance used in PC extraction on the DGV accuracy for seven traits in TEST bulls is reported in Figure 2. Basically, correlations between

DGV and DRPF exhibit a slight linear increase with increasing amounts of extracted components. This behavior can be observed for almost all traits except fat percentage. Thus the value of explained variance further considered in the study was 99%, with a corresponding number of 15,199 extracted components.

Pearson correlations between predicted DGV and DRPF in TEST bulls for the different estimation methods are reported in Table 1. Values were low to moderate and different among traits and, to a lesser extent, among methods. Smallest accuracies were obtained for reproduction traits, especially calving ease, for which the correlation was 0.05. Milk composition traits, as protein and also somatic cell count showed highest values, ranging from 0.40 up to 0.64. Also some conformation traits as type, udder score and rump angle showed accuracies around 0.50. Yield traits had intermediate values of correlations (about 0.40-0.45).

Slight differences in $r_{DGV,DRPF}$ between methods were observed (Table 1). In general, accuracies of PC_BLUP and BAYES_A (for 21 and 12 traits out of 35, respectively) were slightly higher than those of BLUP method that uses SNP genotypes as predictors. On average, the maximum and the minimum value of accuracy for each trait differed about 0.04. A relevant exception is represented by fat percentage where BAYES_A markedly outperformed the other methods, yielding an accuracy greater than about 0.25 and 0.15 compared to the other approaches. Such a better performance was also observed for fat yieldeven though of a reduced magnitude. .

Comparison between accuracies of genomic predictions and of pedigree indexes shows a slight superiority for most of traits for genomic predictions

Table 2 shows the coefficient of determination (R^2), mean squared error of prediction and its decomposition of DGV calculated with the three methods for some selected traits: protein yield, fat percentage, somatic cell count, longevity, fertility, stature and udder support. The PC_BLUP

235 method showed the lowest values of MSEP across all the considered traits. Moreover, as far as the
236 decomposition of the MSEP was concerned, for almost all traits this approach was characterized by
237 the lowest incidence of components related to prediction bias, i.e. mean bias (on average 13% of the
238 MSEP) and inequality of variances (22%), and highest for incomplete covariation (66%) and
239 random error (85%), i.e. the sources of random variation. SNP_BLUP and BAYES_A had basically
240 the same composition of the MSEP. Less defined is the pattern across traits. Protein yield, for
241 example, had the highest value for mean bias but the lowest for inequality of variance. In any case,
242 fat percentage and somatic cell count showed the largest incidence of random variation.

243 Regression coefficients ($b_{DGV,DRPF}$) of DGV on DRPF are shown in Figure 3. A relevant
244 difference between methods can be observed. Values are lower than one in almost all traits for the
245 PC_BLUP method (on average 0.74±0.21), indicating that positive values of DGV overpredict
246 DRPF and vice versa for negative DGV values. On the contrary, all methods that use directly SNP
247 genotypes showed ($b_{DGV,DRPF}$) almost always greater than one (except for calving ease): 1.23±0.35,
248 1.22±0.37, for SNP_BLUP and BAYES_A, respectively. Moreover, among all methods, the
249 PC_BLUP showed the lowest degree of accuracy (Figure 3). A definite pattern across traits could
250 not be identified, except for the very low values for calving ease and the rather high (>1.30) for
251 some conformation traits.

252 **Discussion**

253 As expected, due to the limited size of the reference population, prediction accuracies for
254 direct genomic values were low to moderate. For example, squared correlations reported for US
255 Holstein (VanRaden *et al.* 2009) obtained by used a REF population of 3,576 bulls are on average
256 0.2 higher than those reported in the present work for a set of 23 common traits. Similar differences
257 have been observed with reliabilities reported by Su et al. (2010) on a 3,330 Danish Holsteins. In
258 VanRaden et al. (2009), the R^2 for Net merit has been calculated also with REF population sizes of

1,151 and 2,130. Values were similar to those here reported, i.e. 0.12 and 0.17 vs 0.16, respectively. Accuracies obtained in the present work were similar to those reported by Moser *et al.* (2010) with a REF population of 1,847 bulls. All the above mentioned figures confirm the importance of the reference animals for the realized accuracy of genomic predictions. In any case accuracies of DGV in this study were equal or in many cases higher than realized accuracies of traditional pedigree indexes.

The reduction of predictor dimensionality from 39555 to 15207 by principal component analysis did not reduce accuracy of DGV predictions compared to methods that use directly all SNP genotypes available. In most of cases the PC-BLUP approach gave the best accuracies even if differences from the other methods were rather small. Such results confirm previous reports on simulated (Solberg *et al.* 2009; Macciotta *et al.* 2010) and real data (Long et al., 2011; Pintus *et al*., 2012). The reduction performed in this study was of a lower magnitude compared to some of the above mentioned research, and the number of PC to be retained was not fixed a priori but based on the test of different thresholds of explained variance (the number of PC variables were about 38% of the original variables). However, the effect on computation demand was evident. The average computation time using GSRU for the PC-BLUP method was about 1,21 min (from 1.14 to 2.81 depending on the trait) 2 hours (from 50 min to 4 h depending on the trait), whereas 1 h 36 min (from 59 min to 2 h)whereas 18 hours (from 9 h to 29 h) were needed on average with the SNP-BLUP and BAYES_A approaches using a Linux server with 4 x 4 quad core processors and 128 Gb RAM.

DGV predictions obtained with the PC-BLUP methods were characterized by the lowest bias. This result has been also confirmed by the decomposition of the mean squared error of prediction, that highlighted a less bias for the PC-based method compared to the other approaches Moreover, the comparison between the two BLUP-based methods showed slightly better accuracies

283 for the PC_BLUP than for the SNP_BLUP (magnitude of difference was always lower than
284 8%).These results may be ascribed to better numerical properties of the extracted variables
285 compared to the direct use of SNP genotypes. Actually principal components are uncorrelated and
286 this feature prevents problems of multicollinearity that are likely to occur because of linkage
287 disequilibrium between loci when dense marker genotypes are used as predictors (Long *et al.* 2011).

288 As far as the effect of the assumption on marker effect distribution is concerned, BAYES_A
289 yielded substantially the same accuracies as BLUP methods for almost all traits. These figures do
290 not agree with simulation studies were Bayesian methods performed better than BLUP methods
291 (Meuwissen *et al.* 2001; Habier *et al.* 2007). On the other hand, they are similar to those obtained
292 from real data (Moser *et al.* 2009 ;Su *et al.* 2010; VanRaden *et al.* 2009). A relevant exception is the
293 genomic predictions of fat percentage. For this trait, the accuracy of the BAYES_A method was
294 markedly higher (>30%) than in BLUP methods. A possible explanation can be found in the genetic
295 structure of the trait. It is well known that fat content is largely influenced by single genes with
296 major effect, DGAT1 (Grisart *et al.* 2004). Previous studies reported that methods that assume
297 heterogeneity of variance across chromosome segments usually perform better than those that
298 assume an equal contribution of all markers to the genetic variation in case of traits influenced by
299 few genes.(VanRaden *et al.* 2009; Hayes *et al.* 2010).

300 Some differences across traits were evidenced, although no definite trend between categories
301 (e.g. yield, conformation, udder, etc.) was observed. Highest values were observed for milk
302 composition, for some conformation and yield traits. Lowest values were found for calving ease,
303 fertility and most conformation traits. Such different behavior between traits is in agreement with
304 reports on North American (Schenkel 2009; VanRaden *et al.* 2009; Olson 2011) and German (Liu
305 2011) Holsteins. These figures seems to be related, even if roughly, to the heritability of the trait
306 even if some exception have been observed, as somatic cell count. Liu et al. (2011), partially

307 explained the lower genomic accuracies for traits with low heritability as a consequence of the
308 lower accuracies of their conventional EBV in the REF population.

309

310 **Conclusions**

311 In this work direct genomic breeding values of Italian Holstein bulls for productive and
312 functional traits have been calculated using different methods and types of predictors. Realized
313 accuracies of genomic predictions are low to moderate, conforming the importance of the size of
314 the REF populations. However, DGV accuracies were similar or, in many cases, slightly higher than
315 those of pedigree indexes. The use of dimension reduction techniques did not result in a decrease of
316 accuracy of genomic prediction compared to methods that uses all SNP available. Assumptions on
317 distribution of marker effect had a relevant influence in the efficiency of the genomic selection for
318 traits that are known to be affected by a limited number of genes with a large effect.

319

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402 Table 1. Pearson correlations between predicted DGV and DRPF, for different estimation methods, for the
403 test animals.

	Methods			
Trait	SNP-BLUP	PC-BLUP	Bayes_A	PI
PFT	0.42	0.42	0.39	0.41
Milk Yield	0.43	0.43	0.46	0.45
Fat Yield	0.41	0.42	0.49	0.34
Protein Yield	0.39	0.39	0.38	0.40
Fat %	0.44	0.47	0.64	0.45
Protein %	0.51	0.53	0.55	0.50
SCC	0.54	0.54	0.52	
Longevity	0.34	0.35	0.31	
Fertility	0.27	0.28	0.28	
Type	0.51	0.51	0.51	0.43
Overall Conformation Score	0.43	0.42	0.40	
Overall Udder Score	0.48	0.49	0.46	0.41
Overall Feet & Leg Score	0.35	0.35	0.36	
Stature	0.47	0.48	0.46	0.50
Strength	0.36	0.37	0.35	0.13
Body Depth	0.39	0.41	0.37	0.46
Angularity	0.45	0.44	0.44	0.41
Rump Angle	0.52	0.53	0.49	0.43
Rump Width	0.44	0.42	0.43	0.54
Rear leg side view	0.35	0.35	0.34	0.39
Foot Angle	0.38	0.38	0.37	0.35
Rear leg rear view	0.33	0.32	0.34	
Locomotion	0.45	0.44	0.45	
Fore Udder Attachment	0.45	0.45	0.44	0.38
Rear Udder Attachment Height	0.46	0.46	0.44	0.39
Rear Udder Attachment Width	0.26	0.25	0.26	0.30
Udder Cleft	0.41	0.41	0.41	0.41
Udder Depth	0.43	0.45	0.42	0.37
Front Teat Placement	0.42	0.41	0.41	0.26
Teat Length	0.33	0.34	0.32	0.20
Rear Teat Placement	0.36	0.35	0.36	
Direct Calving Ease	0.05	0.05	0.05	
Maternal Calving Ease	0.04	0.04	0.05	
Production Persistency	0.29	0.30	0.30	
Maturity rate	0.34	0.34	0.34	
Average across traits (n=35)	0.39	0.39	0.39	
Average across traits (PA n=24)	0.42	0.43	0.43	0.39

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406 Table 2. Mean squared error of prediction (MSEP) and its decomposition (%), and coefficient of
407 determination (r^2) of Deregressed Proof on direct Genomic Breeding values for some traits in the
408 PREDICTION animals using different estimation method.

Protein Yield	**r^2**	**MSEP**	**mean bias**	**unequal variances**	**incomplete (co)variation**	**Systematic bias**	**Random errors**
PC-BLUP	0.15	312.20	0.24	0.10	0.66	0.06	0.70
SNP-BLUP	0.15	327.31	0.31	0.15	0.54	0.02	0.67
Bayes_A	0.14	356.88	0.36	0.19	0.45	0.01	0.63
Fat %							
PC-BLUP	0.22	0.04	0.00	0.26	0.74	0.01	0.99
SNP-BLUP	0.19	0.04	0.00	0.38	0.62	0.00	1.00
Bayes_A	0.42	0.03	0.00	0.20	0.80	0.00	1.00
Somatic Cell Count							
PC-BLUP	0.29	25.34	0.01	0.29	0.70	0.00	1.00
SNP-BLUP	0.29	25.75	0.00	0.42	0.57	0.01	0.99
Bayes_A	0.29	26.49	0.00	0.54	0.46	0.04	0.96
Longevity							
PC-BLUP	0.12	63.37	0.22	0.18	0.60	0.03	0.75
SNP-BLUP	0.11	61.55	0.21	0.29	0.49	0.01	0.78
Bayes_A	0.09	61.46	0.19	0.53	0.28	0.01	0.80
Fertility							
PC-BLUP	0.08	81.05	0.09	0.24	0.67	0.04	0.87
SNP-BLUP	0.07	80.04	0.11	0.36	0.54	0.01	0.88
Bayes_A	0.07	82.37	0.14	0.49	0.37	0.00	0.86
Stature							
PC-BLUP	0.23	1.58	0.21	0.27	0.52	0.00	0.79
SNP-BLUP	0.22	1.74	0.27	0.36	0.38	0.01	0.73
Bayes_A	0.20	1.98	0.32	0.41	0.27	0.02	0.66
Udder support							
PC-BLUP	0.17	1.80	0.11	0.21	0.69	0.02	0.87
SNP-BLUP	0.17	1.83	0.14	0.32	0.54	0.00	0.86
Bayes_A	0.16	2.00	0.21	0.43	0.37	0.01	0.79

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411 Figure 1. Distribution of number of bulls per birth year in the reference and test population.

412 Figure 2. Pearson correlations between predicted direct genomic breeding values and deregressed proof, for
413 the PC-BLUP method using a different number of Principal components (PC) explaining the given proportion
414 of the variance, for the PREDICTION animals.

415 Figure 3. Regression coefficients ($b_{DRPF,DGV}$) of Deregressed Proof on direct Genomic Breeding Values
416 estimated with PC-BLUP, SNP-BLUP and BAYES_A methods, and on Parent Average for all traits
417 considered in test animals

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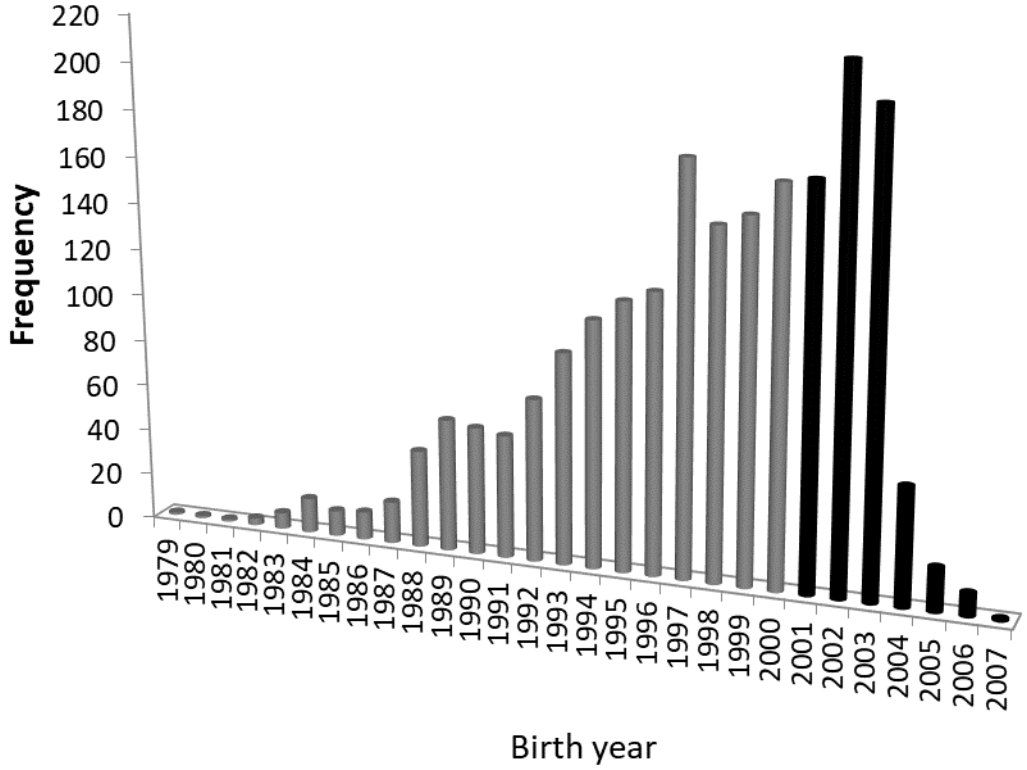

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422 **FIGURE 1**

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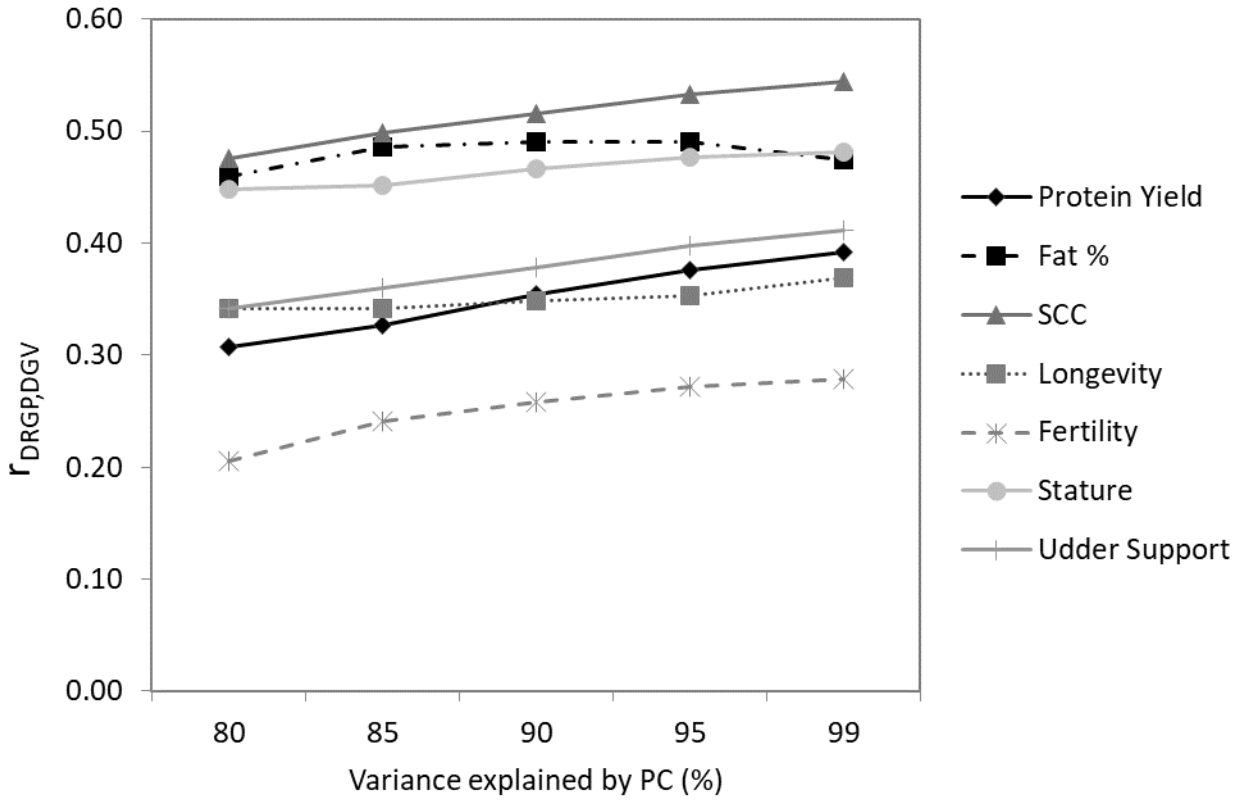

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425 **FIGURE 2**

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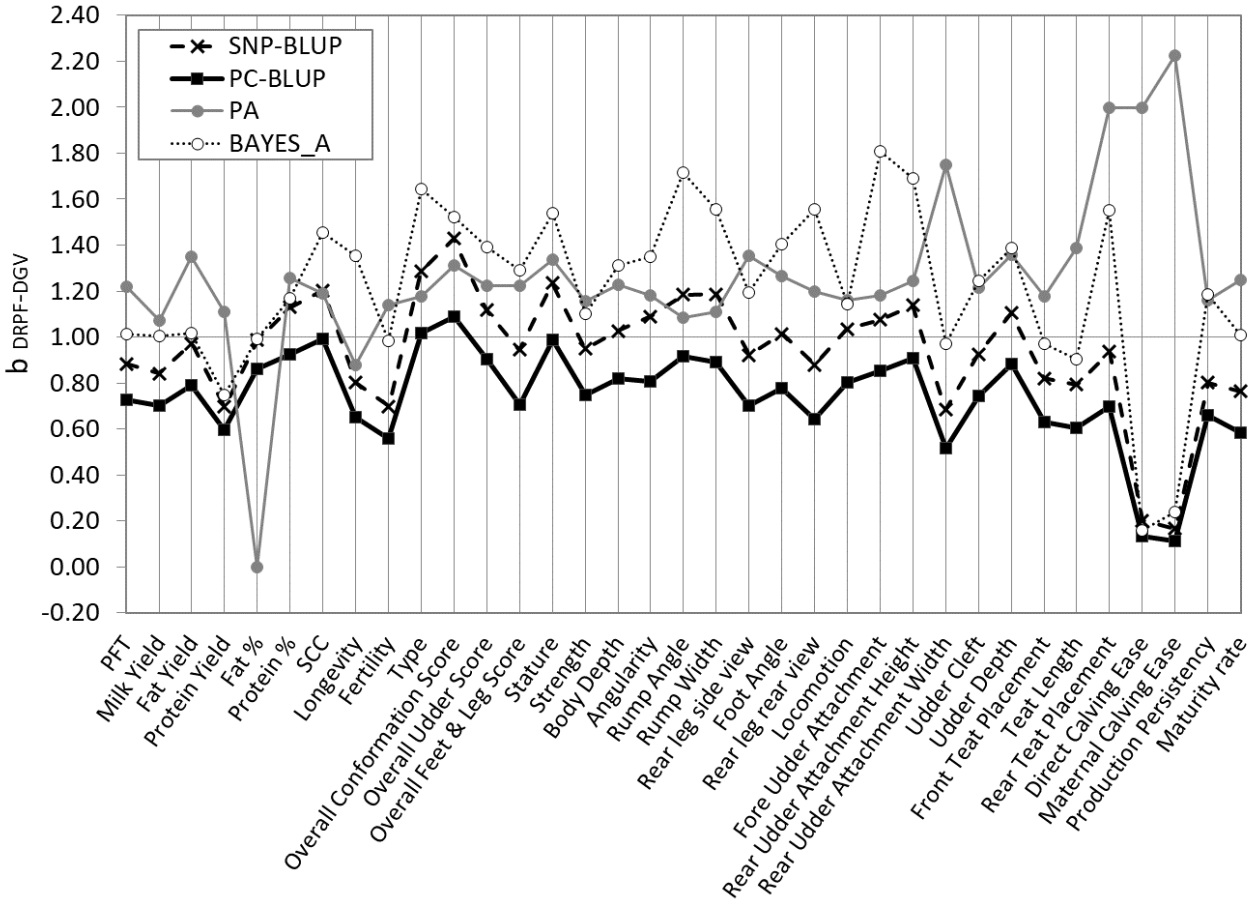

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432 **FIGURE 3**

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